Biological Conservation 160 (2013) 173–182

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment

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ARTICLE INFO

Article history:
Received 15 August 2012
Received in revised form 4 January 2013
Accepted 7 January 2013

Keywords:
Arthropod
Carabid
Landscape connectivity
Early-successional
Invertebrate
Spider

ABSTRACT

Creation of ecological networks is advocated to increase the viability of regional populations and their resilience to climatic and land-use change with associated habitat fragmentation and loss. However, management of network elements should be appropriate for the regional biota conserved, requiring evidence from multiple taxa. We examined the response of carabids, spiders, ants and vascular plants, to six physical disturbance treatments ranging in intensity plus controls, replicated across 63 plots in a plantation trackway network of a heathland region in England. Over 2 years, 73,182 invertebrates from 256 species were identified and 23,241 observations of 222 vascular plant species made.

Abundance and richness of stenotopic carabids and plants (respectively associated with heath and dune, or unshaded physically-disturbed low-nutrient soils) increased with disturbance intensification. Ant assemblages were similar among treatments and control plots, only differing from heathland sites through addition of generalist species. Spider assemblages were less resilient; overall abundance and richness reduced with greater disturbance. Generalist spiders recovered in year two, although incompletely in the most intensely disturbed treatment. Contrasting responses among taxonomic groups likely reflect differences in dispersal ability.

Treatments that merely disrupted vegetation quickly regained plant cover and height, suggesting frequent reapplication will be required to maintain heath specialist species. Turf stripping, the most severe treatment, was quickly colonised by specialist carabid and plant species. Treatments that are more durable may allow stenotopic spider assemblages to develop in contrast to shorter-lived treatments. Effectiveness of early-successional habitat networks within regions supporting European lowland heathland will be enhanced by physical disturbance and turf stripping. Our results emphasise the importance of examining multiple taxonomic groups when assessing management outcomes.

1. Introduction

Land-use change, with associated loss and fragmentation of habitat, provides enormous challenges to conservation biology. In addition, species adapted to narrow habitat and climate niches may struggle to keep up with predicted climate shifts in fragmented landscapes. Ecological connectivity can help mitigate such impacts by enhancing local population resilience (Gilbert-Norton et al., 2010; Haddad et al., 2003) and potentially by facilitating range shift in response to anthropogenic climate change (Heller and Zavaleta, 2009; Krosby et al., 2010; Lawson et al., 2012). Consequently, there is increasing emphasis on restoring connectivity in strategic conservation policy (Lawton et al., 2010; Mitchell et al., 2007; Natural England, 2011). However, effective implementation requires understanding what functional groups form regional priorities for conservation (Dolman et al., 2012) and which management techniques enhance landscape permeability for these. To optimise connectivity in modern landscapes, there is a pressing need to examine how management affects network suitability for contrasting taxa of conservation concern.

Mechanisms of dispersal within ecological networks depend on the temporal and spatial scale of species' life-histories (Bennett, 2003). For relatively mobile species, facilitating individual dispersal can link discontinuous populations even if connecting elements are sub-optimal relative to the discrete habitat patches that support reproduction (Haddad and Tewksbury, 2005). In contrast, for many arthropods and plants of limited dispersal ability, percolation of resident populations requires networks of appropriate habitat quality (Bennett, 2003). Examining the occurrence of taxa among network elements that differ in habitat structure and management can therefore provide evidence to enhance network quality, without the necessity to demonstrate movement.

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http://dx.doi.org/10.1016/j.biocon.2013.01.006

European heathland assemblages are of high biodiversity value and protected under the EC Habitats Directive (EC, 1992), but over the last two centuries European lowland heathland has been reduced by 60–94%, primarily by afforestation and agricultural conversion (Farrell, 1989; Gimingham, 1972). Remnants are often small and isolated (Piessens et al., 2005; Webb, 2009). As many early-successional heathland species are dispersal-limited, isolated populations are vulnerable (Bonte et al., 2003; Piessens et al., 2005; Webb and Hopkins, 1984), consequently, efforts to reconnect heathland are important to conserve its biodiversity in the longer term (Hopkins and Webb, 1984; Lawton et al., 2010). The importance of dispersal for invertebrate populations of fragmented open-habitats is well known (de Vries et al., 1996; Turin and den Boer, 1988; Warren et al., 2001), yet we usually lack understanding of the appropriate vegetation structure or management to enhance connectivity. Many stenotopic heath species require physical disturbance that creates ruderal resources and sparse early-successional structures (Buchholz, 2010; Dolman et al., 2012). With increasing evidence that stenotopic invertebrates inhabit and percolate along trackways or road verges (Eversham and Telfer, 1994; Noordijk et al., 2011), including those within tree plantations (Bertoncelj and Dolman, in press; Pedley et al., 2013), there is potential to use disturbance treatments to enhance ecological connectivity by taking advantage of existing trackway networks. However, robust evidence across multiple taxa is first required.

The objective of this study is to determine the most effective disturbance treatment to conserve early-successional specialist heathland species by enhancing landscape connectivity. We examined the response of carabid, spider, ant and vascular plant assemblages to physical disturbance treatments in trackways within an afforested landscape in eastern England planted over lowland heathland, fallowed and marginal croplands. Within the forest 1290 km of trackways provide a network that has potential to connect both the permanent and ephemeral open habitats within the forest landscape, and to link external heathland remnants across the forest. The invertebrate and plant response to a range of treatments that differ in disturbance intensity was examined in terms of assemblage composition, richness and abundance of early-successional specialist and generalist species; invertebrate assemblages were also compared to reference heath sites.

2. Materials and methods

2.1. Study site

Thetford Forest was planted in the early 20th century and occupies 185 km^2 of Breckland in eastern England (0°40′E, 52°27′N). Breckland is characterised by a semi-continental climate, sandy, nutrient-poor soils and a long history of grazing and episodic cultivation (Dolman and Sutherland, 1992) supporting a regional biota that includes coastal, continental and Mediterranean elements. Physically disturbed heathland and ruderal habitats support at least 542 priority species (rare, scarce, range-restricted or UK Biodiversity Action Plan species) (Dolman et al., 2012). The forest is dominated by conifer plantations, with 80% comprised of Corsican (*Pinus nigra*) and Scots (*Pinus sylvestris*) pine, managed by clearfelling (typically at 60–80 years) and replanting of even-aged patches (planting 'coupe': mean area 9.0 ha ± 8.6 SD) creating a coarse-grained mosaic of growth stages. Coupes are subdivided by a network of forestry trackways that provide management access. Trackways comprised two elements: central wheelings with sparse vegetation and exposed substrate, flanked by vegetated verges that are cut annually to facilitate access but lack bare substrate. Trackways vary in width (mean 13.7 m ± 5.8 SD, range 5–50 m, sample size $n = 93$), substrate (sand and gravel), vegetation and shading due to adjacent tree height. Approximately 50% of heathland associated carabid species have been recorded from this trackway network (Lin et al., 2007) as well as many characteristic heathland spider species (Pedley et al., 2013); however, some of the region's rarest and most exacting species appear absent.

2.2. Physical disturbance treatments

Six physical disturbance treatments that varied in intensity plus a set of non-managed controls, each replicated nine times across a total of 63 plots (treatment plot length 150 m, width minimum 4 m, maximum 5 m), were established within the trackway system in February 2009. Plots were distributed within the contiguous core area of Thetford Forest (comprising four management 'blocks'), and in one large southern forest block (Fig. 1). Treatments included two cutting treatments: swiping (S, sward cut with tractor mounted blades, clippings left in situ) and harvesting (H, sward cut and removed with silage harvester) and four soil disturbance treatments ranging from mild disruption by discing (D, tractor-pulled disc harrow, disrupting but not destroying vegetation with shallow soil disturbance, 10–20 cm deep), to moderate disturbance by forest ploughing (FP, soil and litter inverted in plough lines producing bare mineral substrate in the furrow, width 30–40 cm, depth 40–50 cm, alternating with 40–50 cm wide strips of intact vegetation), heavy disturbance by agricultural ploughing (AP, turf and top-soil inverted producing bare-substrate across the plot, with biomass retained and buried to 20–30 cm), and the most destructive treatment turf stripping (TS, removal of vegetation, root mat, litter and organic soil, exposing mineral subsoil at a depth of 15–30 cm).

Plots were placed within trackways at least 9 m wide, within coupes aged 10–25 years that comprise closed-canopy stands, which lack open habitat carabids (Bertoncelj and Dolman, in press), spiders (Pedley, unpublished data) or plants (Eycott et al., 2006a). To reduce shading effects plots were established in the widest verge of trackways oriented north–south, or the northern verge of trackways oriented east–west. All plots were located a minimum of 100 m away from other treatments, open areas, forest restocks and felled coupes to ensure samples were not capturing open-habitat species from adjacent habitats. The soil in each plot was initially classified as acidic (podzols and acidic brown earths), or calcareous (rendzinas, calcareous sands, and mixed calcareous–acidic periglacial complexes) from soil maps (Corbett, 1973). This was validated by sampling soil in August 2009, with four cores (4.75 cm in diameter, 5 cm deep, excluding the root mat and undecomposed litter) taken from each plot, air-dried and passed through a 2 mm sieve; 50 g from each core were mixed with 125 cm^3 of distilled water and pH measured with an electronic meter.

Treatments were allocated randomly to suitable trackways, stratifying between (1) acidic soils lacking bracken *Pteridium aquilinum*, (2) acidic soils dominated by bracken, and (3) calcareous soils. Treatments were not clustered within the geographic spread of plots (latitude $F_{6,56} = 1.014$, $P = 0.426$; longitude $F_{6,56} = 1.396$, $P = 0.232$); however, to control for any geographic effects on biotic composition, forest block was examined as a categorical factor in analyses.

2.3. Invertebrate sampling in treatment plots

In both 2009 and 2010, ground-active invertebrates were sampled in each plot on three occasions: in May, June and late July/early August. In each period, six pitfall traps (each 7.5 cm deep, 6.5 cm diameter, filled with 50 ml of 70% ethylene glycol) set 15 m apart in a single transect along the centre of each plot (beginning 37.5 m from each end) were opened for seven consecutive

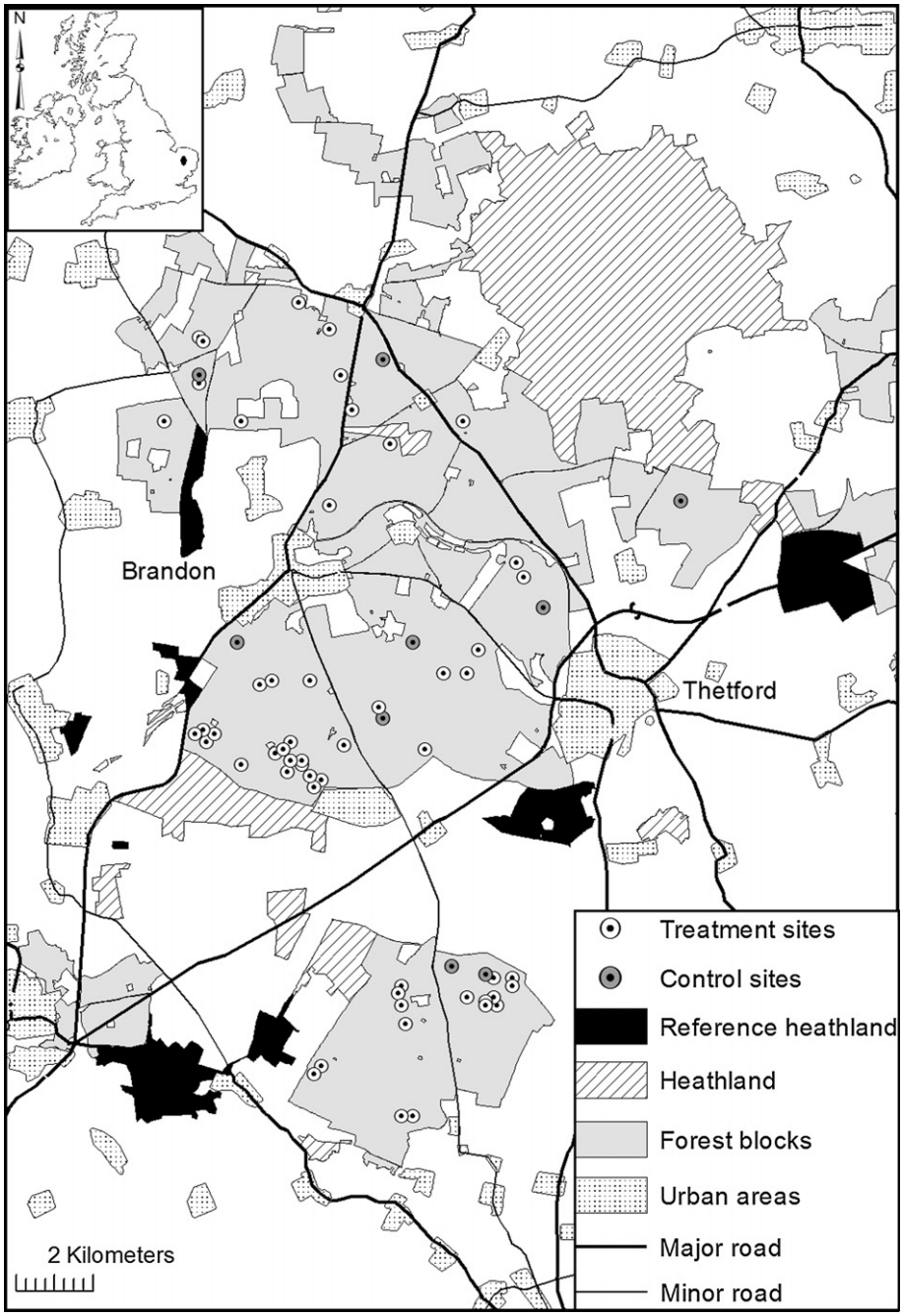

Fig. 1. Sample locations within Thetford Forest showing the distribution of treatment and control transects and sampled reference heathlands.

days. Traps in each transect were combined giving one composite sample per plot-year. Taxonomic references for subsequent species identification of carabids, ants and spiders are detailed in Appendix Table A1.

2.4. Invertebrate sampling in heath reference sites

Ground-active invertebrates were also sampled on eight heath reference sites located within 8 km of treatment plots, of which seven were designated under EU and or UK conservation legislation. All were subject to conservation management, predominantly rabbit and sheep grazing, with some mechanical disturbance (for site details see Appendix Table A2). Within each site, three transects were set (each of six pitfall traps of the same dimensions used in experimental plots) at least 50 m apart, open for seven consecutive days over three trapping periods (May, June and August) in 2009.

2.5. Plant species composition and vegetation structure

In each treatment plot, incidence of vascular plant species was recorded from 20 1 m × 1 m quadrats placed regularly along the centre, between May and August of both 2009 and 2010. In August of both years, vegetation height in each plot was assessed at 40 points using a sward stick (diameter 90 mm, weight 250 g, following Dolman and Sutherland (1992)), and percentage of bare substrate visually estimated in 20 cm × 20 cm at each point. Due to protected nesting birds it was not possible to survey vegetation

structure or vascular plant composition on heathland reference sites.

2.6. Classification of species

For each taxonomic group, we classified species as those likely to be ubiquitous in the forest (eurytopic and or woodland species: hereafter 'generalist shade-tolerant'), and stenotopic species of regional conservation interest, for which treatments may enhance connectivity (hereafter 'specialists'). Specialist invertebrates were defined as species associated with dry grassland, lowland heathland, dunes, chalk or gravel pits. Effects of treatments were contrasted between generalists and specialists; less exacting species of open mesic habitats (such as moorland) were not considered further but generally maintained an even abundance across treatments.

Vascular plants were classified as those that are shade tolerant and or occur in mesic (damp or nutrient-enriched) habitats ('generalist shade-tolerant'), and specialist species restricted to oligotrophic (low nutrient) open-habitats that also require physical disturbance (i.e. ruderals, annuals, or species intolerant of competition in closed swards); these are a conservation priority in the region (Dolman et al., 2012). Vascular plant species capable of persisting in open nutrient-poor habitats without regular disturbance are ubiquitous throughout the trackway network and were not considered further. Species lists, sources for habitat classification and protection status are shown in Appendix Table A1.

2.7. Data analysis

Abundance measures comprised: frequency of each vascular plant species (per plot; range 0–20), and numbers of individuals per plot-year for invertebrates, pooled across pitfalls and sampling periods.

Sampling effort and species richness were compared among treatments and reference sites with sample-based rarefaction using the EstimateS software package (Colwell, 2009).

For each taxonomic group, assemblage composition across treatments and heath reference sites was examined using Non-Metric Multidimensional Scaling (NMDS) performed on a matrix of Bray–Curtis dissimilarities of abundance data (square root transformed and Wisconsin double standardization) using the vegan package (Oksanen et al., 2010) in the statistical software R (R Development Core Team, 2012). Centroids for heath reference samples and treatments were plotted to visualise assemblage differences. Stress values were examined to assess the accuracy in

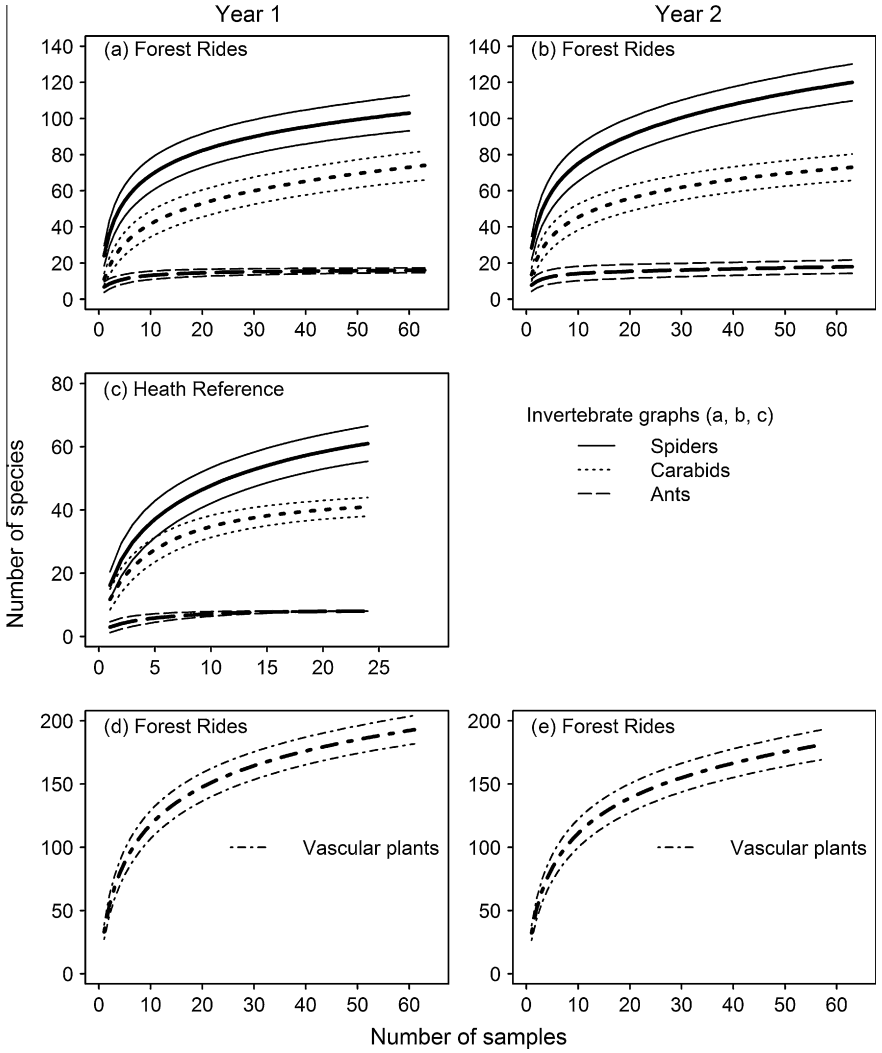

Fig. 2. Sample-based rarefaction curves with 95% confidence intervals for pitfall catches of ground active invertebrates and quadrat sampling for vascular plants, shown separately for each year of sampling. (a and b) pitfall trap sampling from treatment and control plots of invertebrate taxa; spiders, carabids and ants; (c) invertebrate sampling of heath reference sites (in year one only); (d and e) vascular plant sampling from treatment and control plots.

representation: <0.05 excellent; <0.1 good; <0.2 potentially useful; >0.3 close to arbitrary (Clarke and Warwick, 1994). The influence of soil pH on plant assemblage NMDS axis scores was examined by Spearman's correlation.

To examine the stability of sampled communities between years, NMDS was also performed simultaneously on data from both years of treatment sampling and heath reference sites sampled in year one only. Paired *t*-tests were used to investigate differences in the ordination scores of control plots between each sampled year. NMDS axis one scores of control plots indicated stable invertebrate and plant compositions between years (paired *t* tests: $P > 0.05$). The large differences between years in ordination of treatments relative to reference sites are therefore unlikely to be an artefact of inter-annual variation in weather.

Species richness and abundance of specialists and generalist shade-tolerant species were compared among treatments and heath reference transects using generalised linear models (GLMs) in R. The appropriate error term (normal, Poisson, negative binomial) for each analysis was selected by comparing Akaike's Information Criterion (AIC) and examining the ratio of deviance/residual degrees of freedom. Differences among site category means (treatments and controls) were examined by Tukey pairwise comparisons. GLMs retained soil type (categorical: acidic, calcareous and mixed) and forest block when significant ($P < 0.05$). Spatial autocorrelation of GLM residuals was examined by Moran's I in the ape package v.3.0–6 (Paradis et al., 2004) in R. In all instances Moran's I was not significant ($P > 0.05$).

Sward height and the extent of bare substrate were also compared among site types (treatments, heath references and controls) over the 2 years using GLMs. Only those site types that contain more than one percentage bare substrate and sward heights greater than zero were included in the analysis.

3. Results

A total of 73,182 invertebrates from 256 species were identified over the 2 years, comprising 7564 carabids from 94 species, 24,087 spiders from 142 species and 41,531 ants from 20 species. In addition, 23,241 observations of vascular plants from 222 species were recorded. Sampling of ground-active invertebrates and vascular plants effectively captured the assemblage composition, as sample-based rarefactions approached their asymptote (Fig. 2). Species richness was lower for all invertebrate groups in heath reference transects than in treatment plots (Fig. 2). Fourteen species were unique to heathlands, eleven of which were specialists including six nationally scarce species, three ground spiders and three carabids.

3.1. Vegetation structure

Control and cutting treatments provided very little bare substrate over the duration of the experiment (Fig. 3). As expected, the four soil disturbance treatments provided a significantly greater extent of bare substrate compared to controls in the first year. However, by year two the extent of exposed substrate in disced

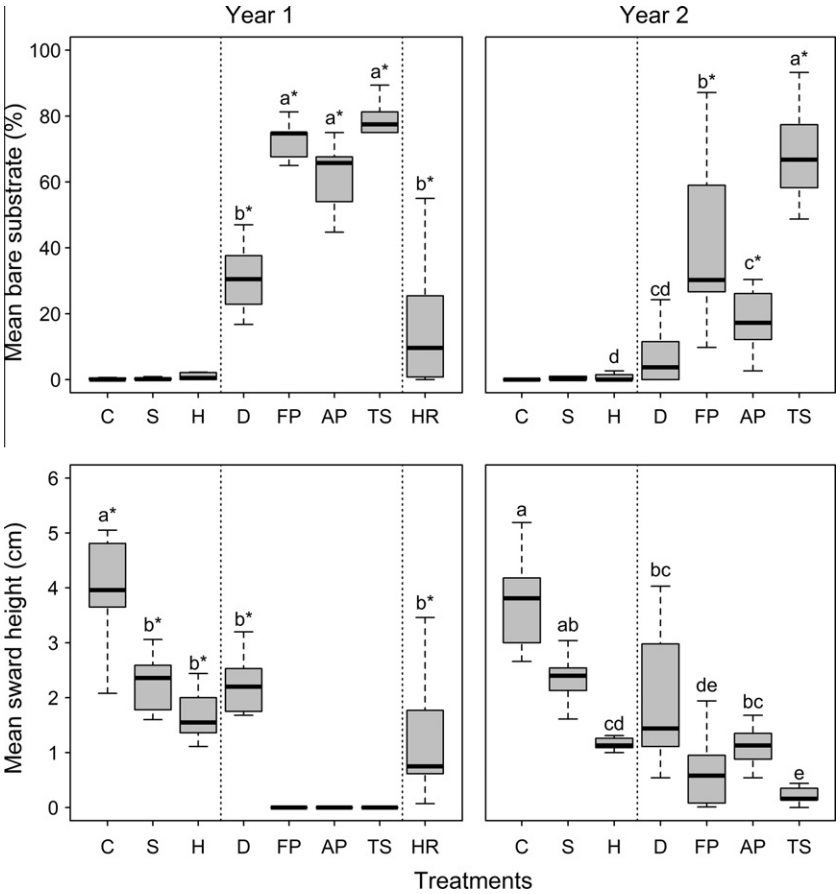

Fig. 3. Response of sward height and extent of bare ground to disturbance treatments: C = control, S = swipe, H = silage harvest, D = discing, FP = forest plough, AP = agricultural plough, TS = turf strip, and in HR = heath reference. Vertical dotted lines separate control and cutting treatments from soil disturbance treatments and heath reference sites. Results of generalised linear models (χ^2 and *p*-value) comparing site types are presented; means that share a superscript (homogenous sub-sets, a–e, ranked highest to lowest) do not differ significantly (Tukey pairwise comparisons $P < 0.05$). Treatments with negligible bare substrate (<1%) or mean sward height of zero were excluded from GLMs due to heteroscedasticity; means marked with an asterisk have confidence interval that does not overlap with these zero reference classes.

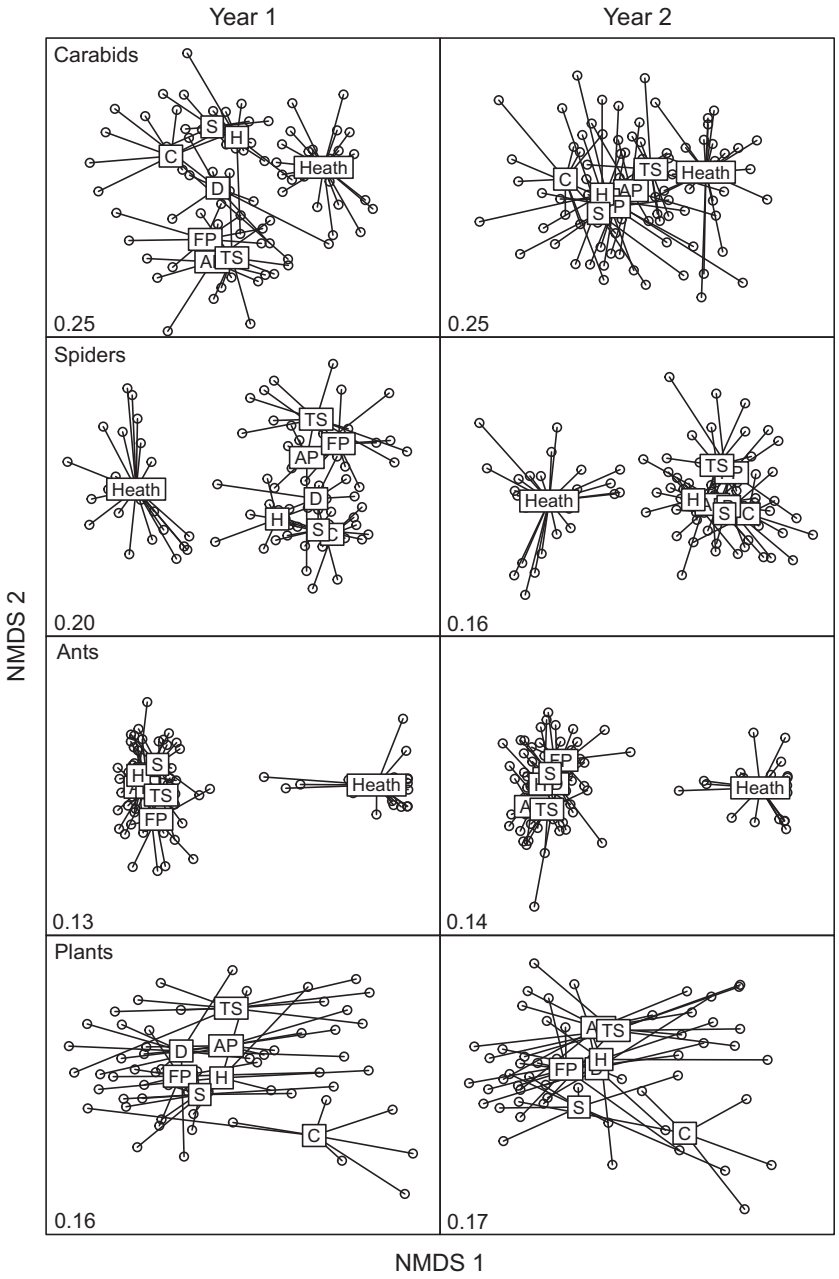

Fig. 4. Non-Metric Multidimensional Scaling (NMDS) ordination comparing assemblage composition of three invertebrate groups and vascular plants among seven disturbance treatments and heath reference transects. Points are sampled transects with lines connecting to habitat centroids (C = control, S = swipe, H = silage harvest, D = discing, FP = forest plough, AP = agricultural plough, TS = turf strip, Heath = heath reference). Stress values for each ordination are show at the bottom of each plot.

plots was similar to that in control and cutting treatments, while turf-stripped sites retained more bare substrate than any other treatment in the second year. Sward-height was reduced in the three most destructive treatments (FP, AP, and TS) in year one compared to control and cutting treatments (Fig. 3). However, by year two sward-heights only remained significantly lower in turf stripped plots. Sward-height and percentage of exposed substrate was variable in samples from heath reference sites due to differing levels of physical disturbance (Fig. 3).

3.2. Composition of carabid assemblages

NMDS ordination showed carabid assemblages in treatment plots differed from heath reference assemblages in year one, but in year two many of the turf stripped and agricultural plough plots were located in a similar part of the ordination space to heath transects (Fig. 4). Pooled abundance of specialist species increased with increasing intensity of disturbance; only turf stripped plots did not continue this upward trend in the first year but still contained twice the abundance of control plots (Fig. 5). This pattern of response continued in the second year, turf stripped plots had accumulated significantly greater abundance and richness of specialist species than controls (Fig. 5 and Fig. 6). Although single records of a species should be considered quasi-anecdotal observations, it is notable that the two specialist Red Data Book (RDB) species recorded in the experiment (RDB1 endangered *Amara fusca*, RDB2 vulnerable *Harpalus froelichii*) were found in turf stripped plots in year two.

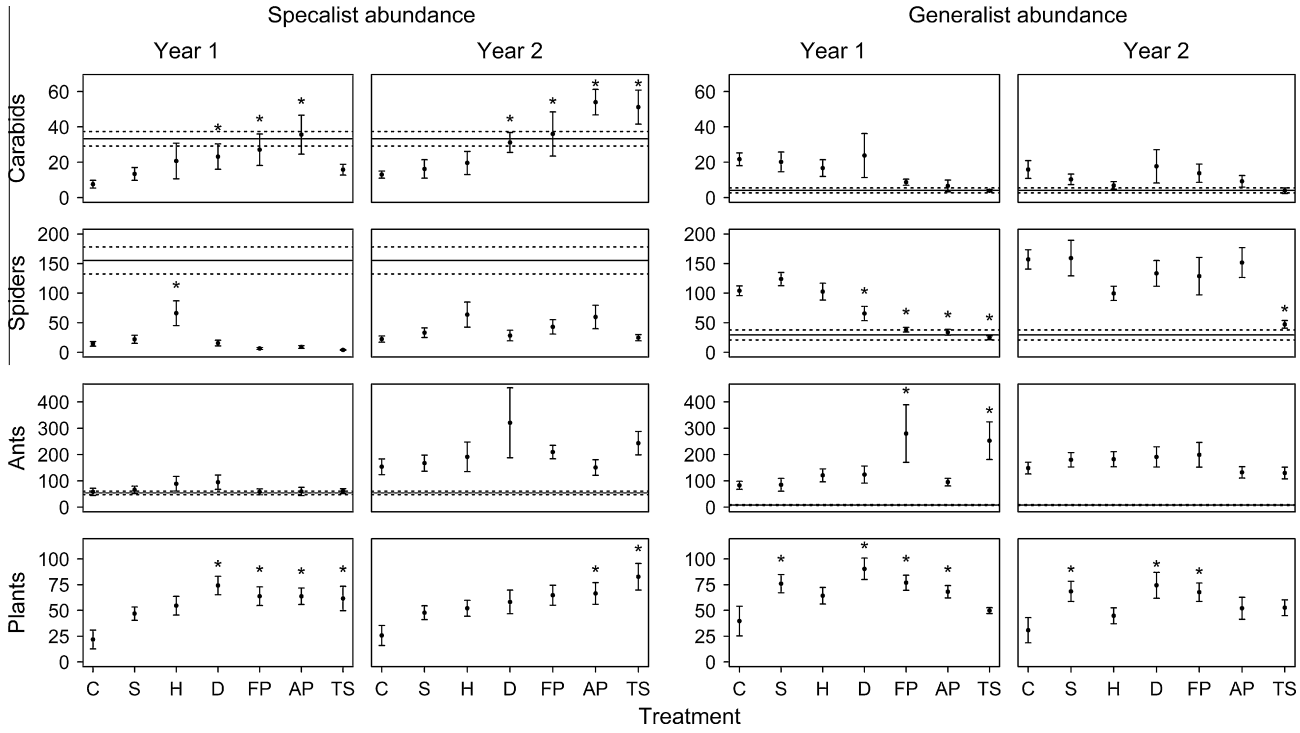

Fig. 5. Mean and standard error of species abundance across disturbance treatments and controls for specialist (left) and generalist shade-tolerant species (right). Mean (horizontal line) and standard error (dotted line) of invertebrate groups sampled in heathland reference sites in 2009 are also shown. Generalised linear models (χ^2 and *p*-values are shown in Appendix Table A3) were used to compare among treatments and controls. Tukey pairwise comparisons were used to define homogenous sub-sets; treatments that are significantly different from controls ($P < 0.05$) are shown with an asterisk.

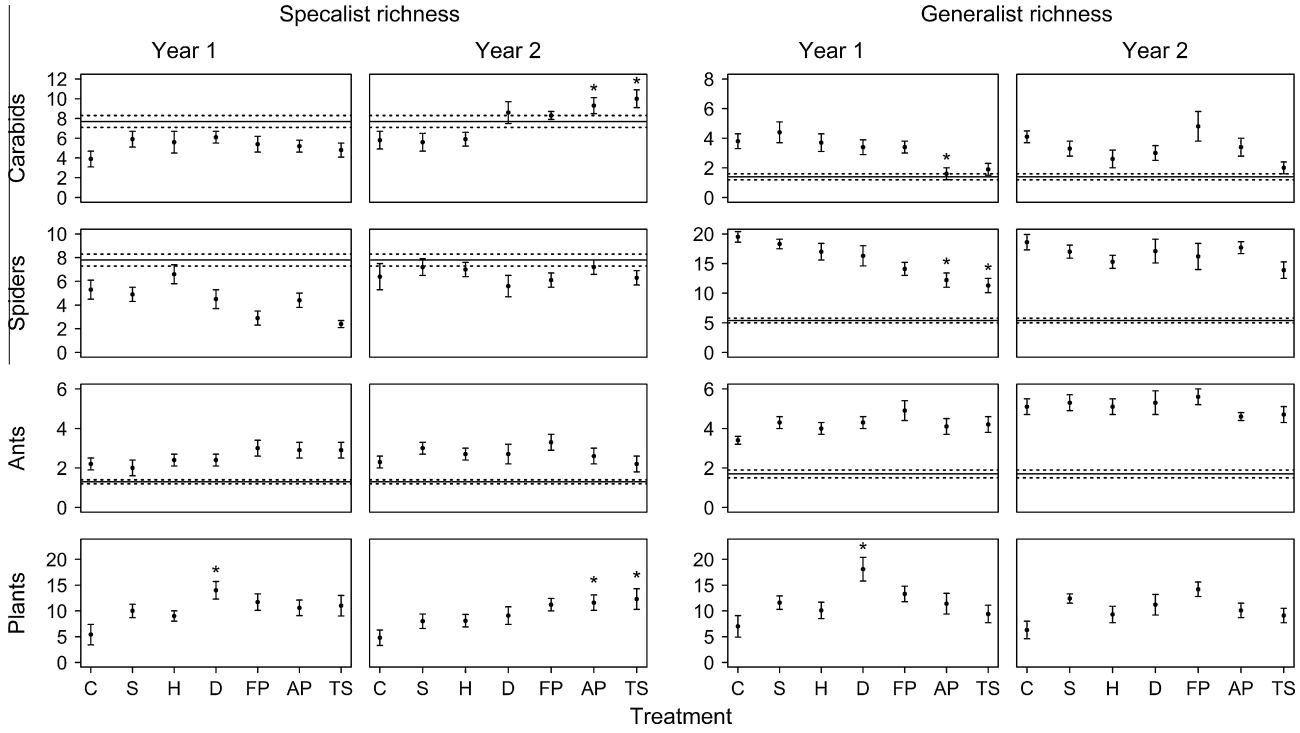

Fig. 6. Mean and standard error of species richness across disturbance treatments and controls for specialist (left) and generalist shade-tolerant species (right). Mean (horizontal line) and standard error (dotted line) of invertebrate groups sampled in heathland reference sites in 2009 are also shown. Generalised linear models (χ^2 and *p*-values are shown in Appendix Table A3) were used to compare among treatments and controls. Tukey pairwise comparisons were used to define homogenous sub-sets; treatments that are significantly different from controls ($P < 0.05$) are shown with an asterisk.

3.3. Composition of spider assemblages

Composition of ground spider assemblages differed between treatment plots and heath reference transects, with substantial differences along axis one of the NMDS in both years (Fig. 4). Pooled abundance of specialist species was one or two orders of magnitude greater in heath reference transects than in treatment plots (Fig. 5). In addition, heath transects had lower richness and abundance of generalist shade-tolerant species. Compared to controls, the three most destructive treatments (FP, AP, and TS) had reduced richness of specialist species and reduced abundance and richness of generalist shade-tolerant species in year one (Fig. 5 and Fig. 6). However, in the second year all intensely disturbed treatments, except turf stripping, had recovered in abundance of generalist shade-tolerant species and all treatments had similar species richness of both specialists and generalists.

3.4. Composition of ant assemblages

Ant species composition of heath reference transects differed to that of treatment plots in both years along axis one of the ordinations (Fig. 4). Species richness of heath transects was low compared to treatment plots (Fig. 2 and Fig. 6) and all species found in heaths were also recorded in treatment plots. Species composition among all treatments was similar (Fig. 4) and no significant differences in species richness were recorded between treatments in either year (Fig. 6 and Appendix Table A3).

3.5. Composition of vascular plants

Composition of vascular plant assemblages in the NMDS was strongly influenced by soil pH, with calcareous plots located to the right on the first axis (Fig. 4: year 1 $r_s = -0.86$, $p < 0.001$; year 2 $r_s = -0.76$, $p < 0.001$). Species composition differed markedly among treatments with the more intensely disturbed treatments located towards the top of the ordination (Fig. 4). In both years the greatest separation was between turf stripped plots and the controls on axis two.

The pooled abundance of specialist plants increased with intensification of disturbance (Fig. 5). In year one, richness of specialist plants was greater in all soil disturbance treatments than in control and cutting treatments (Fig. 6), with disced treatments having the greatest species richness. However, in year two disced plots had reduced in both richness and abundance of specialist species and were similar to controls. In year two turf stripped and agricultural ploughed treatments contained similarly high abundance and richness of specialist species, both being significantly greater than controls.

4. Discussion

4.1. Enhancing ecological network quality

We examined assemblage responses to management techniques applied in a well-replicated experiment on a network of open-habitat trackways using intensive multi-taxa sampling, recording over 70,000 invertebrates and 23,000 vascular plant observations. Mechanical disturbance treatments enhanced stenotopic early-successional carabid and vascular plant assemblages, with the most intensive disturbance, turf stripping, supporting greater richness and abundance of specialist species. Turf stripping removed the vegetation and organic matter from forest trackways, creating the exposed sparsely-vegetated substrate required by arenicolous (sand inhabiting) and thermophilous species. However, not all taxa responded positively to disturbance; spiders were less resilient while ants were unaffected by treatments at this scale. Invertebrate assemblages in heath reference sites differed from those in treatment plots, but primarily through the lack of generalists and greater abundance of specialists from heath assemblages rather than the absence of specialist species from treatment plots. Where early-successional biota represent a conservation priority, ecological networks could be enhanced through the use of severe physical disturbance.

4.2. Contrasting taxonomic responses

Both richness and abundance of specialist carabids and vascular plants increased with disturbance intensity, contrasting to the abundance and richness of specialist spiders and ants in disturbance plots. The positive responses to disturbance of specialist carabids and vascular plants may in part be due to local dispersal from relictual populations in the trackway network (Bertoncelj and Dolman, in press), for plants supplemented by regeneration from persistent seedbanks (Eycott et al., 2006b) and endozoochorous dispersal by abundant deer (Eycott et al., 2007). These could enable specialist individuals to rapidly take advantage of newly disturbed habitat. However, the presence of rare carabids not previously recorded from the forest landscape indicates that longer distance dispersal may also have contributed to observed responses for this group.

Soil disturbance and vegetation removal alter ground microclimate and reduce soil moisture making habitats less humid, a central habitat characteristic affecting arthropod composition (Entling et al., 2007; Schirmel and Buchholz, 2011). Schirmel and Buchholz (2011) suggested that greater vegetation density and the amelioration of microclimate and soil humidity were the main drivers of successional change in the arthropod assemblage, with a reduction of rare stenotopic species from grey dunes to young birch forest. In this study, turf stripped and agriculturally ploughed sites, characterised by exposed substrate and reduced vegetation density, contained the greatest numbers of specialist carabid species.

Like carabids and vascular plants, source populations of specialist ground spiders also inhabit the forestry trackways (Pedley et al., 2013). The greater vulnerability and slower recovery of ground spider assemblages compared to carabids may therefore reflect differences in both direct mortality from treatment application and differences in dispersal ability. Spider assemblages are known to be vulnerable to grassland management techniques that alter habitat structure (Bell et al., 2001; Morris, 2000). In crop fields, Thorbek and Bilde (2004) showed spiders were more vulnerable through direct mortality from mechanical soil disturbance than were carabid or staphylinid beetles. It is likely that direct mortality explains the large difference in abundance of generalist shade-tolerant spiders found in low, compared to high disturbance plots in the first year.

As well as their vulnerability to physical disturbance, specialist spiders may also be dispersal limited. Although many spiders have the notorious ability to disperse by 'ballooning', using silk threads to catch wind currents, potentially travelling many kilometres (Bell et al., 2005; Thomas et al., 2003), compared to active flight this passive mode of dispersal gives less control over direction and, crucially, where and when to land. This may not be a problem for generalist species. However, in fragmented landscapes, species with specialist requirements may have a low probability of landing in suitable habitat. It is notable that, while ballooning is particularly common among Linyphiids (Bonte et al., 2003), of 286 Linyphiidae species known in Britain only 15 (5%) are associated with inland xeric habitats (Harvey et al., 2002). Similarly, of the 68 Linyphiidae species recorded in this study, only four could be classified as specialists (Appendix Table A1, see also Duffey et al. (1957)); the remainder were regarded as generalists. In addition, stenotopic

spiders from grey dunes in Belgium exhibited low ballooning propensity when tested in laboratory studies (Bonte et al., 2003). Poor dispersal ability of specialist spiders was also suggested by Hopkins and Webb (1984) who found fewer specialist spiders in more isolated heathland fragments in Dorset.

In contrast to spiders, carabids are less reliant on wind currents in flight. Although overall direction may be wind dependent (As, 1984), winged flight permits decisions on elevation, distance and greater control over landing sites. Effective aerial dispersal over many kilometres has been reported for both brachypterous (rudimentary or small winged) and macropterous (large winged) species that colonised islands in the Baltic (As, 1984; Kotze, 2008). For the carabid *Amara plebeja*, van Huizen (1977) reported distinct flight periods with a spring dispersal to grassland reproduction sites that may use wind currents, and an autumn flight to forested hibernation sites. Effective dispersal over kilometres and appropriate seasonal site selection suggests a greater ability to find appropriate habitat.

4.3. Durability of treatment

Responses over 2 years gave some indication of the relative durability of treatments. Bare substrate and short swards are required by much of the threatened biodiversity in dry heathland and low intensity arable regions (Buchholz, 2010; Dolman et al., 2012). In this study, low-impact cutting treatments maintained a relatively short sward but did not provide exposed substrate and provided little benefit to specialist species.

Although the mild soil disturbance provided by discing increased the abundance and richness of specialist plants in the first year, by year two disced plots did not differ from controls and sward height and the extent of bare substrate was similar to that of cutting treatments. Like discing, forestry and agriculture ploughing disrupted but did not remove the vegetation and soil biomass; recovery was again rapid, the extent of bare substrate quickly reduced as sward cover and height increased. To maintain bare substrate and early successional assemblages, such treatments would need repeating at intervals (estimated repetition, for discing every 2–3 years, for ploughing 3–5 years). The depletion of spiders caused by discing and ploughing makes regular reapplication on the same plot less desirable, though adjacent plots could be treated.

In contrast, turf stripped plots retained extensive bare substrate after two growing seasons. Turf removal has been used to create and restore other nutrient-poor early-successional habitats including meadows (Tallowin and Smith, 2001), lowland heath (Allison and Ausden, 2004) and coastal dunes (Grootjans et al., 2002) where mechanical removal of vegetation has been recommended to recharge early-successional arthropod assemblages (Buchholz, 2010; Maes and Bonte, 2006). Although treatment longevity for turf stripping is unknown and will depend on soil fertility (Kondoh, 2001; Noordijk et al., 2010), the effects will outlast less intensive treatments allowing greater recovery time for less resilient populations.

4.4. Conservation implications

To support specialist species of conservation concern we advocate management of connecting elements in early-successional networks using high intensity, long lasting disturbance treatments such as turf stripping, or periodic ploughing of plots in close proximity. Applied within existing heathlands, such treatments could provide valuable heterogeneity augmenting assemblages by providing niches for early-successional specialists. For enhancement of trackways in an agricultural context, intense disturbance may require perennial buffers providing refugia for overwintering and disturbance-sensitive invertebrates. It is likely that treatments with long-lasting benefits will allow recovery of negatively affected spider communities in contrast to comparatively rapid results achieved for specialist carabids and vascular plants. A strength of this study lay in examining responses for contrasting speciose groups of invertebrates and vascular plants; nevertheless, we advise caution in applying results to other taxa, particularly vertebrates. While heathland reptiles may benefit from the creation of basking or oviposition sites through physical disturbance (Dolman and Land, 1995), treatments risk harming overwintering populations and should be applied heterogeneously and at a local scale. Physical disturbance can provide habitat for priority bird species utilising ruderal seed resources or that forage in sparse open vegetation, including characteristic heathland species such as woodlark *Lullula arborea* (Mallord et al., 2007).

Conservation outcomes of physical management have often been examined for just one or a few taxonomic groups (Pywell et al., 2007; Vandvik et al., 2005); however, the contrasting responses in this study demonstrate the importance of studying multiple taxa from diverse trophic levels with differing foraging and social strategies. Extending this approach to understand responses in terms of life history traits and functional attributes of diverse taxa would enhance the understanding of conservation management options and provide greater transferability and generality of outcomes.

Acknowledgements

Experimental treatments were applied by the Forestry Commission. Funding was provided by the British Ecological Society, Forestry Commission, Natural Environment Research Council, Norfolk Biodiversity Information Service, Norfolk Biodiversity Partnership and Suffolk Biodiversity Partnership. We thank the following land owners and managers for allowing sites access: Norfolk Wildlife Trust, Suffolk Wildlife Trust, Elveden Estates, Forest Heath District Council, Natural England and the Forestry Commission. We thank Dr. H. Mossman for comments on this manuscript, Bev Nichols (Natural England) and Neal Armour-Chelu (Forest Commission) for help and support during the study. We are very grateful to Martin Collier (Carabidae), Jake Stone (Carabidae) and Doreen Wells (Formicidae) for identification of invertebrate material.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.01.006.

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